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BIODIVERSITY RESEARCH

Seamount benthos in a cobalt-rich crust region of the central Pacific: conservation challenges for future seabed mining

Thomas A. Schlacher[1]*, Amy R. Baco[2], Ashley A. Rowden[3], Timothy D. O'Hara[4], Malcolm R. Clark[3], Chris Kelley[5] and John F. Dower[6]

[1]*Faculty of Science, Health & Education, University of the Sunshine Coast, Q-4558 Maroochydore, Australia,* [2]*Department of Oceanography, Florida State University, 600 W. College Ave., Tallahassee, FL 3230, USA,* [3]*National Institute for Water and Atmospheric Research - NIWA, Private Bag 14901, Wellington, New Zealand,* [4]*Museum Victoria, PO Box 666, Melbourne, VIC 3001, Australia,* [5]*Hawaii Undersea Research Laboratory -HURL, University of Hawaii, 1000 Pope Rd, MSB 303, Honolulu, HI 96822, USA,* [6]*Department of Biology, University of Victoria, PO Box 1700 Station CSC, Victoria, BC V8W 2Y2Victoria, BC, Canada*

*Correspondence: Thomas A. Schlacher, Faculty of Science, Health & Education, University of the Sunshine Coast, Q-4558 Maroochydore, Australia;
E-mail: tschlach@usc.edu.au

ABSTRACT

Aim The benthic fauna of seamounts typically includes organisms that are slow-growing, long-lived and sensitive to mechanical disturbance, making seamounts susceptible to anthropogenic impacts. Such impacts may arise from mining cobalt-rich crusts, envisaged for seamounts in the central North Pacific; this scenario requires that environmental guidelines for mining operations on seamounts be developed. Here, we provide the biological information essential for effective conservation planning of deep-sea features targeted for such mining.

Location Central North Pacific, Hawaiian Seamount Chain.

Methods Spatial analysis of seamount benthos using a large biological dataset (> 600 taxa) obtained from 144 submersible dives (depth range: 113–1985 m) on 27 seamounts covering a distance of over 2200 km of ocean.

Results Benthic assemblages of invertebrates are structurally different between seamounts located inside and outside a region with cobalt-rich crusts. This spatial contrast results from variations in species composition and relative abundance of species, rather than differences in species richness, challenging historical notions of an impoverished cobalt-rich crust fauna in the region. Seamount assemblages also have high species turnover with depth and distance at the scale of individual seamounts, but geographic separation was a poor predictor of ecological separation for the region at large.

Main conclusion Several implications for the design of spatial management and conservation tools with respect to mining emerge: (1) conservation of seamounts outside the cobalt-rich crust region is unlikely to capture the full range of ecological features found inside the region; (2) conservation areas need to encompass a broad bathymetric gradient; (3) ideally, mining blocks on individual seamounts should not exceed 2 km in length. Overall, the life history characteristics and morphological traits of the deep-water invertebrate fauna typical of seamounts in the region imply that any recovery from mechanical impacts is likely to be very slow.

Keywords
Benthic assemblages, cobalt-rich crust, conservation, deep sea, mining, seamounts.

INTRODUCTION

Seamounts are prominent features of the ocean floor and sites of importance for oceanic processes in the geobiosphere (Clark *et al.*, 2010). Biological assemblages on seamounts vary across a wide range of spatial scales, from structural difference between habitats on individual seamounts, to differences among regions (Richer de Forges *et al.*, 2000; Clark *et al.*, 2010; McClain *et al.*, 2010). How seamount biota are structured spatially remains one of the most

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important science questions, especially in the context of conserving seamount ecosystems that may become threatened by deep-sea mining (Rowden *et al.*, 2010a; Schlacher *et al.*, 2010; Clark *et al.*, 2012; Stocks *et al.*, 2012).

Seamount biota are particularly sensitive and vulnerable to human disturbance and exploitation (Koslow *et al.*, 2001; Clark *et al.*, 2010). Benthic communities on seamounts usually comprise long-lived, slow-growing, and fragile invertebrates (e.g. corals) that have very low tolerances to physical disturbance (Althaus *et al.*, 2009). These biological traits translate into large ecological impacts where fishing practices use gear that comes repeatedly into contact with the seafloor (Clark & Rowden, 2009). It also means that recovery of the fauna may be exceedingly prolonged, likely to take decades to centuries (Williams *et al.*, 2010).

Recently, there has been heightened interest in extracting mineral resources from seamounts (Hein *et al.*, 2010; Martino & Parson, 2012). Polymetallic massive sulphide deposits form on seamounts with hydrothermal venting activity (Herzig & Peterson, 2002; Zhou, 2007), and cobalt-rich ferromanganese crusts (hereafter referred to simply as 'cobalt-rich crusts') occur on sediment-free seamounts, ridges and plateaus (Hein, 2002).

Mining is envisaged for cobalt-rich crusts in the central Pacific Ocean (Hein *et al.*, 2009). Two applications for exploration have already been submitted to the International Seabed Authority (ISA). Whereas a relatively large amount of research has been carried out on the faunal communities associated with hydrothermal vents and massive sulphide habitats (e.g. van Dover, 2000), much less biological information is available for cobalt-rich crust environments. Data on seamount faunas associated with crusts are available from several surveys in the 1980s in the central Pacific Ocean (Kuznetsov & Mironov, 1981; Wilson *et al.*, 1985; Grigg *et al.*, 1987; Mullineaux, 1987; Fukushima, 2007); these studies typically report comparatively low species richness and abundance.

Crusts can have high concentrations of cobalt, manganese and iron (Zhou, 2007), possibly influencing the occurrence and distribution of fauna according to interspecific differences in metal tolerances. The sparse data on the influence of chemical substrate composition on deep-sea fauna are inconclusive: while foraminifera are reported to settle at higher densities on cobalt-rich crust than on basalt substrate (Verlaan, 1992), no clear relationship between faunal and geochemical composition of polymetallic nodules was found by Veillette *et al.* (2007). The paucity of biological information for cobalt-rich crusts, and the possibility that the chemical composition of the crusts influences the composition and abundance of faunal communities on seamounts, has been recognized as a major impediment in developing and examining options for seabed mining operations on cobalt-rich crusts (Koslow, 2007).

The International Seabed Authority (ISA) has the mandate to regulate the exploration for (and the exploitation of) marine minerals of the seabed and subsoil beyond national jurisdiction ('the Area'). The ISA has held a number of workshops since 2000 to review the available information on the geology, oceanography and biology of crustal habitats and to inform the development of environmental guidelines for future mining of cobalt-rich crusts (ISA, 2007). These initiatives have included a compilation and preliminary analysis of faunal data obtained by the Hawaiian Underwater Research Laboratory (HURL) on a range of seamounts along the Hawaiian Seamount chain (Clark *et al.*, 2011); this technical study was preliminary and the findings presented in this study supersede it.

A fundamental part of developing conservation strategies for seamounts threatened by mining is to know the distribution, diversity and composition of biological features likely to be impacted in relation to the spatial configuration of the threats facing them: this is the principal rationale for this study. We address two main questions: (1) What are the main environmental drivers of spatial variability in the structure of assemblages on seamounts in the central Pacific? and (2) Are benthic assemblages on seamounts in a cobalt-rich region in the central Pacific different from those outside the region?

METHODS

Faunal data

Data come from the HURL submersible (Pisces IV and Pisces V) and ROV video-logging database and were extracted from dives conducted in the Hawaiian Archipelago and nearby seamounts between 1983 and 2007. Data collected by other vehicle types (i.e. the remotely operated RCV-150 and the submersible Makali'i) were excluded because Clark *et al.* (2011) showed that data collected with these platforms clearly differ from those collected with the Pisces submersibles. The data used for this study thus comprise 144 dives at 27 sites (Fig. 1; Table S1 in supplementary material). Site refers to an individual seamount, bank or oceanic island feature (hereon collectively referred to as 'seamounts').

Individual data records represent 5-min sequential observation periods within the continuous video recording made during each submersible dive. All fauna larger than 2–3 cm were annotated and classed as operational taxonomic units, hereafter termed 'taxa' in this study. To ensure taxonomic consistency across dives and sites, identification was carried out by one of us (CK), with help from taxonomic experts as required (see Acknowledgements).

The abundance of taxa in each 5-min observation interval was originally scored according to a three-level ordinal scale: '1' = 1–5 individuals, '2' = 6–10 individuals, and '3' = >10 individuals. The sample unit for the analysis was a dive, composed of variable numbers of 5-min observation intervals. To obtain numerically consistent assemblage data for each dive, observation scores were translated into relative abundance ranks as follows: any taxon for which more than five individuals were observed at least once in a dive was assigned an abundance rank value of '2', all remaining taxa

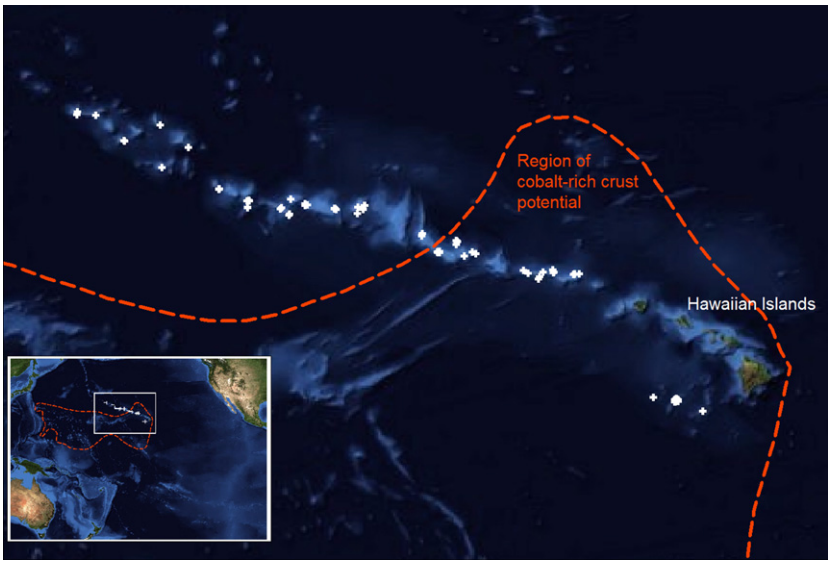

Figure 1 Map showing the position of dives at sites in and outside a cobalt-rich crust region (defined by Hein *et al.*, 2009) in the vicinity of the Hawaiian archipelago (inset shows position of the study area in the Pacific Ocean).

recorded at less than five individuals on the dive were scored as a '1'. Thus, the final abundance ranks reflect whether a taxon was absent (rank = 0), present in comparatively low numbers throughout a dive even when consistently found (rank 1) or comparatively more abundant (rank 2). This method of assessing relative abundance therefore reflects whether a taxon was *ever* more abundant than any other taxon on a dive while also preserving a measure of abundance (i.e. unlike the drastic reduction that a presence/absence transformation would entail). Technically, we adopted this ordinal scale because it is not possible to obtain an absolute measure of abundance or frequency of occurrence at the scale of the sampling unit (i.e. a submersible dive) because of variability in the speed of the submersible and changes to the field of view that may occur within and between the 5-min observation intervals making up a dive. From the full dataset, we culled all records that were not benthic invertebrates.

Environmental data

Seafloor characteristics were described using three complementary properties: (1) principal substratum type and particle size (e.g. sediment, pebbles, cobbles, boulders, bedrock, man-made), (2) bottom topography or relief (e.g. ledges, pillow lava extrusions) and (3) substratum composition (e.g. basalt, mudstone, limestone). To convert these qualitative classes from visual observations into values suitable for numerical analysis, we first scored the observational data for relative hardness (soft/unconsolidated = 0, hard = 1), size (sediment = 0, pebble = 0.25, cobble = 0.5, boulder = 0.75, bedrock = 1) and for relief (low = 0, medium = 0.5, high = 1). Because the substratum data are associated with individual biological records, the amount of data varied depending on the number of taxa recorded per 5-min observation interval. To obtain an unbiased descriptor of seafloor characteristics which is representative of a whole dive, we first calculated the mean score within each 5-min observation window and then averaged across all these mean values that made-up a dive ('mean of the mean' or grand mean).

To generate a single metric for substratum type, we ran a principal component analysis (PCA) of the hardness and size values for all dives. This analysis indicated that the first axis of the PCA accounted for 65% of the total variation, and thus, the score of this axis could be used as a quantitative value for substratum type. The same type of PCA analysis (first axis accounted for 50% of total variation) was used to derive a single metric for substratum composition per dive: here, the underlying data were values of the relative frequency of occurrence of sediment, basalt, mudstone and limestone per dive.

Dive records contained annotations on whether manganese crust was observed on the seafloor. The presence of crust is of interest in examining whether it is correlated with variation in the structure of benthic assemblages. Whether the observed crusts had high or low cobalt content, or were of a particular thickness, however, is not known. In the absence of such data, the presence of manganese crusts themselves remains a useful proxy for cobalt-rich crusts. Thus, substratum data for each record were scored to obtain a metric for crust occurrence (manganese crust = 1, no crust = 0), and the grand mean was calculated as for data on relief and substratum size to obtain a measure of 'Mn-crust prevalence' in each dive.

Whether a dive occurred in or outside a prime region for the development of thick, cobalt-rich crust was determined by reference to Hein *et al.* (2009). Data for seafloor temperature (°C), salinity (‰), and oxygen (ml l^{-1}) were obtained from the CARS2009 dataset, which contains mean values, standard deviations and seasonal coefficients created by averaging/interpolating available global oceanographic cast data (including ARGO float data) for 79 depth layers at a resolution of 0.5° latitude/longitude (Ridgway *et al.*, 2002)

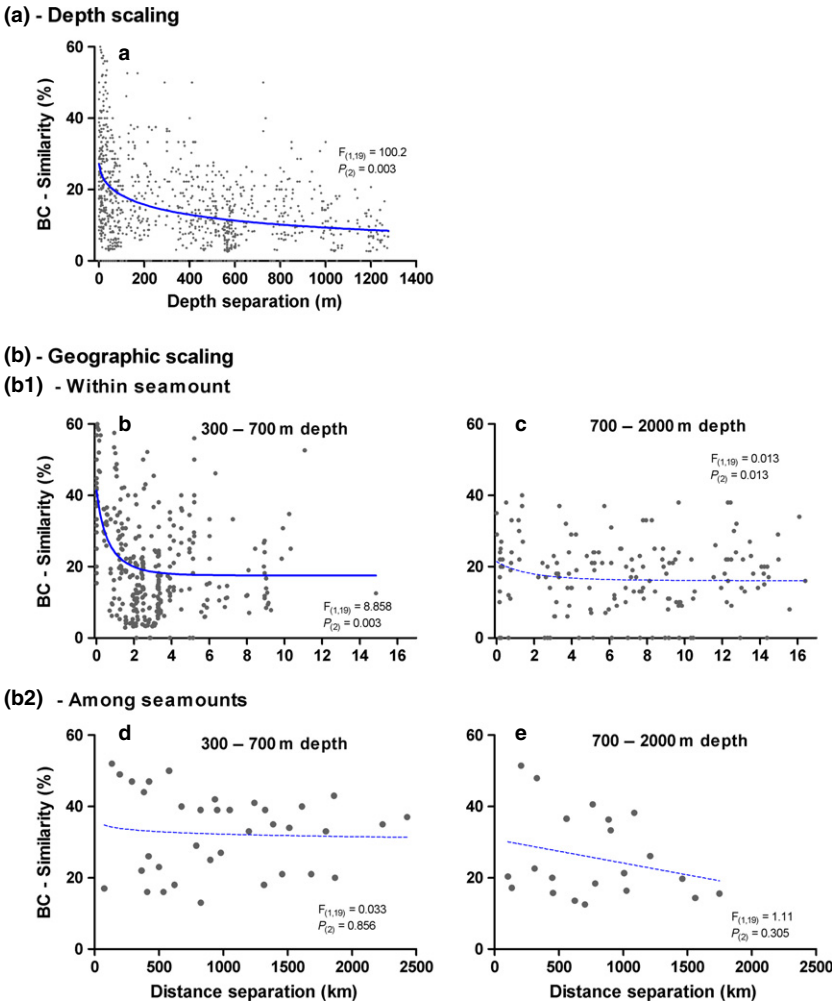

Figure 2 Taxa turnover (dissimilarity of assemblage structure between dives) in relation to (a) separation of dives by depth and (b) separation of dives with increasing geographic distance at the scale of a single seamount (Cross-seamount that had the highest sampling coverage to allow for this analysis) and the scale of seamount-to-seamount differences, BC = Bray Curtis similarity coefficient.

(http://www.marine.csiro.au/~dunn/cars2009/). Values for these variables for each dive were calculated by trilinear interpolation between the fine-scale depth layers, scaled by the actual median latitude/longitude/depth recorded for each dive. Particulate organic carbon (POC; g m^{-2} $year^{-1}$) flux to the seafloor for each dive was estimated from equations fitted to sediment trap data derived by Lutz *et al.* (2007), but using mean and standard deviation primary productivity generated from a Vertically Generalized Production Model algorithm (Behrenfeld & Falkowski, 1997) from 8-day SeaWiFS chlorophyll data for the years 2003–2010 (http://www.science.oregonstate.edu/ocean.productivity/).

Data analysis

The numerical analysis had two purposes: (1) to examine which environmental variables are potential drivers of spatial variation in the seamount fauna; this was performed with distance-based linear models (DISTLM), and (2) to test whether geographic variation in faunal assemblage structure broadly matches the cobalt-rich division of the study area (based on Hein *et al.*, 2009); this comparison was made with permutational analysis of variance (PERMANOVA; McArdle and Anderson, 2001). Prior to DISTLM and PERMANOVA, we conducted diagnostics on the putative effects of sampling effort and depth; details of these diagnostics are provided in Appendix S1.

The relationship between variation in the structure of benthic assemblages and environmental variables was explored using distance-based linear models, DISTLM (McArdle & Anderson, 2001). The contribution of each environmental variable in the DISTLM analysis was assessed using a multi-model inference approach, where AIC weights were summed for each variable across all models in which the variable was present, thereby giving relative probabilities of variable importance (Burnham & Anderson, 2002; Burnham *et al.*, 2011). We ran models on the full dataset, and then separately for each of the three depth strata identified by the cluster analysis (Fig. S1).

The Permanova model employed sequential (Type 1) sums of squares and contained four terms entered in the following sequence: Depth (covariate), Principal Investigator (fixed), Submersible Type (fixed) and Location (i.e. inside and outside the cobalt-rich crust region, fixed).

RESULTS

Spatial variation in benthic assemblages and environmental drivers

At the scale of individual seamounts, taxa turnover between dives was substantial across gradients of depth and geographic distance (Fig. 2). Similarity of assemblage structure declined exponentially with increasing bathymetric separation of dives (Fig. 2a) and for dives that were more distant on the same seamount; this spatial scaling of assemblage change was more pronounced for intermediate depths than for deep samples. For both depth strata, there was a noticeable increase in the rate of taxa turnover at approximately 1–2 km separation between dives within a seamount (Fig. 2b). At the scale of comparisons among different seamounts, there was a much weaker increase in taxa turnover with geographic distance for assemblages in the intermediate depth strata, whereas the increase with distance was more pronounced for the deep stratum (Fig. 2).

No distinct 'best' model emerged from the four DistLM analyses (AIC for all models was <0.1), thus justifying our multi-model inference approach for assessing relative variable importance. Overall, the variable contributions were high (> = 0.45), indicating that models with many predictor variables had a higher AIC despite the penalty that this index imposes on the inclusion of additional variables. The analysis using the full dataset emphasized salinity (0.97), oxygen concentration (0.85) and longitude (0.78) as key predictors (Table 1). There was little variability in predictor contributions (0.48–0.56) for the shallow dives; the higher values were for salinity (0.56) and longitude (0.54). Oxygen (0.77), substratum relief (0.76) and the prevalence of manganese crust (0.67) were emphasized at intermediate depths. At the greatest depths, longitude (0.67) was the most important predictor, followed by prevalence of Mn-crust (0.54) and substratum type (0.53).

Difference between assemblages inside and outside the cobalt-rich crust region

Geographic differences in the structure of the seamount benthos broadly corresponded with the spatial distribution of the conditions permissive for the development of thick, cobalt-rich crusts in the central Pacific: the benthos of sites inside the cobalt-rich crust region differed significantly in terms of species composition and abundance, from sites outside this region (Pseudo-$F = 4.04$, $P < 0.001$, Table 2). Differences in assemblage structure (Fig. 3) were due to different relative abundances of taxa rather than higher numbers of taxa in either region or more taxa being restricted to a single region.

Of the 252 taxa that occurred jointly in both regions, 61% (153 taxa) were more abundant outside the cobalt-rich crust region (Table 3). This pattern of higher abundance outside the cobalt-rich crust region was more pronounced for deep dives (98 of 135 taxa), but reversed for shallow dives where 14 of 22 taxa were more abundant inside the cobalt-rich crust region (Table 3). Taxa that contributed most to structural differences between benthic assemblages inside and outside the cobalt-rich crust region encompassed a broad array of taxonomic groups, including hard- and soft corals, crustaceans, echinoderms, sponges and sea pens (Table 4).

Based on species accumulation curves, we did not find substantial variation in taxa richness that was consistent with a classification of sites being located in or outside the cobalt-rich crust region (Fig. 4). Similarly, for the same level of sampling effort, the number of taxa that were unique to a single region (i.e. occurring inside the cobalt-rich crust region but not outside and *vice versa*) was comparable (Fig. 5).

DISCUSSION

Spatial variation in benthic assemblages and environmental drivers

Invertebrate communities vary in structure, species composition, and diversity among seamounts at both local and regional scales. At local scales, differences in macro- and megafaunal assemblages have been found to occur at scales of < 15 cm (Levin *et al.*, 1986), 10–1000 m (Kaufmann *et al.*, 1989), 1–10 km (Long & Baco, 2013) and > 10 km (Piepenburg & Müller, 2004). At regional scales, geographic variability in seamount fauna has been described in the North Atlantic for polychaetes (Gillet & Dauvin, 2000, 2003;

Table 1 Relative probabilities of variable importance for the full dataset (all dives) and three depth layers separately, derived from summing model weights from every DistLM model that contained each variable. Variable order in the table according to the average rank across the four models listed

Variable	All samples	Shallow dives (100–300 m)	Intermediate dives (300–700 m)	Deep dives (700–2000 m)
Longitude	0.78	0.54	0.64	0.67
Oxygen	0.85	0.53	0.77	0.48
Prevalence of manganese crust	0.67	0.50	0.67	0.54
Substratum type	0.69	0.53	0.62	0.50
Salinity	0.97	0.56	0.54	0.47
Relief	0.67	0.50	0.76	0.47
POC flux to the seafloor	0.67	0.50	0.56	0.51
Substratum composition	0.52	0.52	0.45	0.53
Depth	0.66	0.48	0.60	0.48

Table 2 Summary of permutational multivariate analysis of variance (PERMANOVA) contrasting the structure of seamount assemblages between dives located inside and outside the cobalt-rich crust region. The model used sequential (Type 1) sum of squares and included Depth as a covariate. The primary test of interest is to examine the effect of 'Location' (highlighted), after accounting for the effects of depth, submersible type and the principal investigator

Source	d.f.	SS	MS	Pseudo-*F*	*P* (perm)	Unique permutations
Depth (covariate)	1	36,863	36,863	13.38	<0.001	998
Principal investigator	7	10,1220	14,460	5.25	<0.001	997
Submersible type	1	5822	5822	2.11	<0.001	996
Location (in or outside the cobalt-rich crust region)	1	11,135	11,135	4.04	<0.001	998
Residual	122	336,140	2755			
Total	132	491,180				

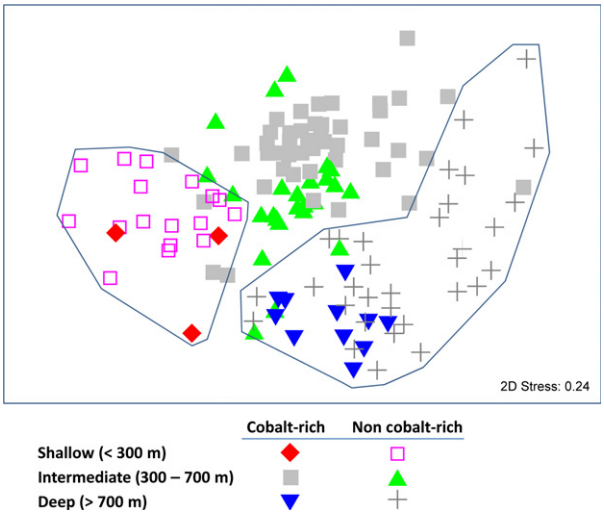

Figure 3 Ordination (non-metric multidimensional scaling) comparing benthic assemblage structure among dives inside and outside the cobalt-rich crust region at three depth strata (cf. Fig. S1 for depth strata classification).

Surugiu *et al.*, 2008) and corals (Hall-Spencer *et al.*, 2007) over distances of 100s of km, reporting up to 70% dissimilarity between seamounts. In the South-west Pacific, the relationship between spatial separation of seamounts and biotic similarity of the fauna has been examined for mixed invertebrate assemblages at distances up to 3000 km by Richer de Forges *et al.* (2000). Subsequent studies on molluscs (Samadi *et al.*, 2006; Castelin *et al.*, 2010, 2011), galatheids (Rowden *et al.*, 2010b) and ophiuroids (O'Hara *et al.*, 2008) in the same general region reported an effect of geographic distances of 100s to 1000s of km on the degree of resemblance among assemblages. O'Hara *et al.* (2010) found that species composition changed along the 950 km Vitoria-Trindade seamount chain in the western South Atlantic. These recent studies emphasize that it is difficult to generalize about the geographic scales over which faunal assemblages of seamounts are structured.

The results of our analyses show that distinct differences in assemblages on a seamount are often not evident at distances < 2 km, possibly due to overlap of monospecific beds at this scale. Patterns of taxa turnover at distances > 2 km within a seamount were most pronounced for assemblages at intermediate (300–700 m) water depths. The pattern of taxa turnover with distance was very gradual across the region. Turnover rates across the region were highest among assemblages on the deepest seamounts (700–2000 m), but even for these seamounts geographic separation was a poor predictor of assemblage dissimilarity.

Our analyses revealed that a broad suite of environmental variables are potential drivers of assemblage structure on seamounts in the region. These drivers include hydrographic conditions as well as seafloor characteristics – a result similar to comparable studies elsewhere (e.g. O'Hara *et al.*, 2010; Rowden *et al.*, 2010b). Of particular interest for this study was that the prevalence of Mn-crust was identified as one potential determinant of benthic assemblage structure on seamounts in the region. However, the likely influence of Mn-crust (as suggested by our modelling) is comparable to that of other properties of the seafloor (e.g. relief, topography, hardness) and thus must not be viewed in isolation. Nevertheless, this result does provide some support for the contention that the presence of Mn-crusts has an influence on the structure of benthic assemblages (Pratt, 1967; Grigg *et al.*, 1987).

Difference between assemblages inside and outside the cobalt-rich crust region

We found a significant difference in assemblage structure in and out of the cobalt-rich crust region. This difference was not driven by a higher number of taxa being unique to the cobalt-rich crust region nor, as implied by the work of Grigg *et al.* (1987), a lower number of taxa in the cobalt-rich crust region. Rather, the difference results mainly from difference in abundance scores of taxa in each region. Although the abundance estimates are based on simple visual abundance scores, our data indicate that more taxa are likely to be less abundant inside the cobalt-rich crust region, particularly on deep seamounts. Whether the relatively low abundance scores of benthic fauna on cobalt-rich crusts are a result of the chemical nature of the crusts remains to be determined, but these findings provide support for Grigg *et al.* (1987)

Table 3 Classification of biological records with respect to the abundance of taxa inside or outside the cobalt-rich crust region

	Shallow (100–300 m) Dives No. Taxa	Intermediate (300–700 m) Dives No. Taxa	Deep (700–2000 m) Dives No. Taxa	All dives No. Taxa
Higher abundance				
Outside cobalt-rich crust region	8 (36%)	79 (56%)	98 (73%)	153 (61%)
Inside cobalt-rich crust region	14 (64%)	46 (33%)	34 (25%)	77 (31%)
No difference in abundance between regions	0 (0%)	16 (11%)	3 (2%)	21 (8%)

who found that the fauna of Mn-crusts can occur in comparatively lower numbers. However, we strongly stress that more quantitative data (encompassing more seamounts and depths) on the density of deep-sea fauna on seamounts in the region are needed to make definitive statements about whether benthic fauna occurs at greater or lesser density in the cobalt-rich crust region; this will also need to encompass data on the chemical composition of the seafloor, which closely match the faunal records spatially.

Linkages to conservation: recommendations

The International Seabed Authority (ISA) is progressing plans to provide guidance to future mining contractors through the development of environmental guidelines (ISA, 2007), and has progressed regulations for prospecting and exploration (ISA, 2012). As part of its responsibility under UNCLOS, the ISA is charged with ensuring effective protection of the marine environment from the effects of mining activities, and the protection and conservation of the flora and fauna of the marine environment. In recently developing an Environmental Management Plan for the Clarion-Clipperton Zone (an area of manganese nodule abundance in the eastern Pacific), it was acknowledged that best-practice generally involves the use of spatial management tools, including the protection of areas thought to be representative of the full range of habitats, biodiversity and ecosystem structure and function within the management area (ISA, 2011).

The cobalt-rich crust regulations further emphasize minimizing impacts on vulnerable marine ecosystems, in particular those associated with seamounts and cold-water corals. How such protected areas should be designed for cobalt-rich crusts was not within the scope of this study, but our results are informative with regard to possible management and conservation options. Accepting that spatial planning is likely to be the prime tool to regulate mining on seamounts, the results from this study are particularly relevant, and on that basis, we offer the following observations and recommendations:

1. Assemblage dissimilarity was strongly influenced by depth. It is therefore important that any spatial management includes protected areas at different depths (e.g. within each of the depth strata identified here for the central Pacific seamounts). Ideally, entire seamounts that have a wide depth range should be conserved.

2. At the spatial scale of seamount-to-seamount differences, geographic distance is a poor predictor of ecological separation. This implies that if entire seamounts are the basic unit of spatial conservation measures, these units need to be dispersed very widely throughout the region to capture the range of geographic variability of the fauna: single seamounts within the central Pacific region are unlikely to be ecologically representative of neighbouring seamounts. Conversely, the lack of a strong relationship between geographic distance and ecological separation does not in itself justify a conclusion, or recommendation, that seamounts identified as candidates for inclusion in conservation areas should not be widely dispersed. On the contrary, while it may be, theoretically, possible to capture a significant part of biological heterogeneity with relatively closely spaced seamounts, the resulting spatial configuration would be more vulnerable to stochastic and human disturbance effects than more widely scattered seamounts.

3. At the scale of individual seamounts, sites separated by more than approximately 1–2 km are likely to have benthic assemblages that differ considerably in community structure. If small-scale spatial conservation areas are considered for individual seamounts, these should be dispersed more than 2 km apart to capture this ecological heterogeneity within the seamounts.

4. The structure of biological assemblages is significantly different on seamounts located in and outside the cobalt-rich crust region. This means that applying spatial conservation measures only to seamounts outside the region is unlikely to capture the full range of biological features present in the cobalt-rich crust region. If the management objective is to protect representative ecological communities, seamounts within the cobalt-rich crust region will need to be conserved.

5. Benthic communities on seamounts in the central Pacific study area were often dominated by corals and sponges. These filter-feeders are highly susceptible to sedimentation that can clog their filtration structures, or smother their early life history stages. Studies and modelling within the Clarion-Clipperton manganese nodule region indicated a scale of up to 100 km for sediment plume dispersal and settlement. How far sediment plumes will disperse from cobalt-rich crust mining operations is unknown. What is clear, however, is that spatial planning measures must consider the scale of the 'downstream' effects of sediment plumes or other hazards (e.g. toxins created by mining operations and carried in

Table 4 List of taxa that contributed most to distinguishing assemblages located inside and outside the cobalt-rich crust region. Listed are the top 10 taxa based on to their contribution to between-region dissimilarity based on SIMPER analysis. Bold values denote higher relative abundance scores in pairwise comparisons. Av Ab = average abundance score (i.e. '1' = 1–5 individuals, '2' = > 5 individuals), which is a relative measure of density (cf. methods section for details)

Common name	Higher Taxon	Taxon	Outside Co-rich crust region (Av. Ab)	Inside Co-rich crust region (Av. Ab)	Contribution (%)
All depths					
Black corals	Anthipatharia	*Stichopathes*	**0.91**	0.25	2.14
Sea pens	Pennatulacea	Pennatulacean	**0.94**	0.31	1.87
Shrimp	Decapoda	Natant Decapod	**0.89**	0.67	1.76
Anemone	Actinaria	Anemone	**0.77**	0.36	1.57
Soft coral (precious coral)	Alcyonacea	*Corallium* sp.	**0.74**	0.48	1.50
Soft coral (sea fan)	Alcyonacea	Gorgonian	0.70	**0.96**	1.46
Gold coral	Zoanthidea	Gerardia sp.	0.47	**0.65**	1.42
Soft coral (sea fan)	Alcyonacea	Primnoid	0.26	**0.60**	1.19
Glass sponges	Hexactinellida	Hexactinellid	**0.51**	0.46	1.18
Brittlestars	Ophiuroidea	Ophiuroid	0.40	**0.43**	1.14
Shallow (100–300 m) dives					
Black corals	Anthipatharia	*Antipathes* sp.	0.18	**1.33**	5.05
Sea pens	Pennatulacea	Pennatulacean	0.76	**1.33**	3.78
Soft coral (sea fan)	Alcyonacea	Gorgonian	0.29	**1.00**	3.59
Black corals	Anthipatharia	Antipatharian	0.29	**1.00**	3.21
Sea urchins	Echinoidea	*Stylocidaris rufa*	**0.76**	0.67	3.19
Black corals	Anthipatharia	*Stichopathes*	**1.65**	1.00	3.09
Sea pens	Pennatulacea	Pennatulacean 'white'	0.35	**0.67**	3.02
Soft coral	Alcyonacea	*Siphonogorgia collaris*	0.35	**0.67**	2.83
Sea urchins	Echinoidea	*Micropyga tuberculata*	**0.76**	0.00	2.60
Sea stars	Asteroidea	*Ctenophoraster hawaiiensis*	0.35	**0.67**	2.52
Intermediate (300–700 m) dives					
Soft corals (precious corals)	Alcyonacea	*Corallium* sp.	**1.16**	0.50	2.04
Anemone	Actinaria	Anemone	**1.12**	0.44	2.04
Gold coral	Zoanthidea	*Gerardia* sp.	1.00	**1.16**	1.82
Shrimp	Decapoda	Shrimp	**1.04**	0.74	1.81
Black corals	Anthipatharia	*Stichopathes*	**0.80**	0.40	1.69
Sea pens	Pennatulacea	Pennatulacean	**0.92**	0.32	1.68
Brittle stars	Ophiuroidea	Gorgonocephalid	**0.76**	0.02	1.44
Sea pens	Pennatulacea	*Calibelemnon symmetricum*	0.52	**0.64**	1.42
Glass sponges	Hexactinellida	Hexactinellid	**0.76**	0.40	1.41
Soft corals (bamboo corals)	Alcyonacea	*Lepidisis olapa* cf	**0.64**	0.10	1.40
Deep (700–2000 m) dives					
Sea pens	Pennatulacea	Pennatulacean	**1.27**	0.21	2.16
Soft corals (bamboo corals)	Alcyonacea	*Lepidisis* sp. cf	**1.90**	0.21	1.60
Glass sponges	Hexactinellida	*Poliopogon* sp.4	**0.91**	0.34	1.44
Sea cucumbers	Holothuroidea	*Paelopatides* cf *retifer*	**0.64**	0.50	1.38
Shrimp	Decapoda	Decapoda Natantia	**0.91**	0.63	1.34
Shrimp	Decapoda	*Aristaeopsis edwardsiana*	**0.64**	0.21	1.26
Glass sponges	Hexactinellida	*Sericolophus hawaiicus*	**0.55**	0.50	1.25
Soft corals (precious corals)	Alcyonacea	*Corallium* sp.	**0.82**	0.50	1.24
Sea cucumbers	Holothuroidea	*Orphnurgus* sp.	**0.55**	0.00	1.23
Golden corals	Alcyonacea	*Iridogorgia magnispiralis* cf.	**0.91**	0.39	1.20

plumes), and establish adequate buffer zones between the mining and conservation areas.

6. Contrary to accepted wisdom, we found no strong evidence that the fauna of cobalt-rich seamounts contains fewer species or is composed of species with different distributions. Thus, there appears to be little justification for allocating less conservation effort to cobalt-rich seamounts based on biodiversity criteria.

7. The biological characteristics of many of the groups recorded in our study mean that recovery from disturbance is likely to be limited and slow. Previous studies on the effects of trawling on seamount communities dominated by

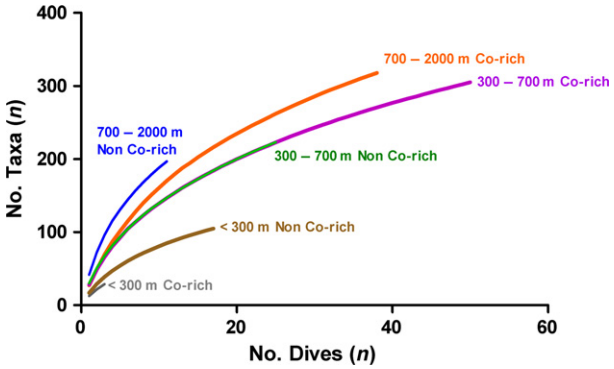

Figure 4 Species accumulation curves contrasting taxon richness between dives inside and outside the cobalt-rich crust region for three depth strata.

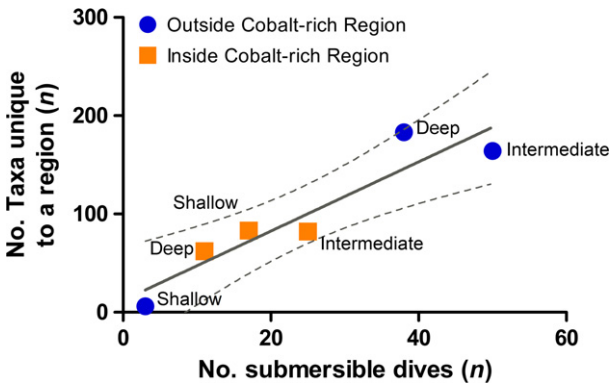

Figure 5 The number of taxa occurring only in a single region (i.e. restricted in their occurrence to either the cobalt-rich crust region or the non-cobalt-rich crust region) in relation to the number of submersible dives at shallow (100–300 m), intermediate (300–700 m) and deep (700–2000 m) depths.

corals found no evidence of recovery after a decade or more (Williams *et al.*, 2010). Mining operations will cause much greater physical impacts to the seafloor habitats than trawling and hence any recovery of the fauna is predicted to be more protracted.

CONCLUSIONS

Although we found clear spatial patterns in the composition of the seamount fauna in the central Pacific that have conservation implications for seamounts targeted for future resource exploitation, we caution against extrapolation of all findings to other areas of commercial mining interests in the deep sea. Some of the general lessons and recommendations coming from this study will be important for other areas, but conservation and management plans need to be site-specific and based on extensive and robust scientific evidence obtained for a specific situation; these studies may also widen the taxonomic ambit beyond the benthic macrofauna investigated here.

Spatial planning measures for conservation have been proposed by the ISA in relation to the mining of cobalt-rich crusts, based on Hein *et al.* (2009) who developed a mine-site model. This model is based on identifying multiple sub-blocks or '*mine sites*' within a seamount, each mine site being 20 km^2, and a total area of about 260 km^2 (or 13 mine sites) being needed for a 20-year commercial operation. These mine sites would be identified following exploration within 18 larger blocks (each 100 km^2) distributed among a 'confinement area' (300,000 km^2) within the region of cobalt-rich crusts. Hein *et al.* (2009) gave a hypothetical example with mine sites distributed over four seamounts (of six initially 'explored'), two of which are adjacent. In their example, mine sites were on the summits of the seamounts, at approximately the same water depth, and clustered in contiguous groups of 2–5. Hein *et al.* (2009) estimated that only about 4% of the total surface area of a seamount <2500 m would be mined. This type of mining site structure has been adopted in the ISA regulations (ISA, 2012).

We conclude by noting that some of the results of our study (summarized above, 1–3) could be used by the ISA to refine the mine model of Hein *et al.* (2009) by including spatial planning strategies to conserve seabed biodiversity. For example, result 1 (species composition of the seamount fauna is strongly determined by depth) highlights concerns over concentrating mine sites at similar depths. Hein *et al.* (2009) estimated that only a small proportion of the seamount would be mined using their model. However, within the narrow depth stratum in which the mine sites are to be concentrated a much greater proportion of the seabed, and therefore the assemblages specific to this depth horizon, would be affected by mining. Thus, to protect assemblages unique to certain depth strata it may be better to consider distributing mine sites over as wide a depth range as possible within and among seamounts. Result 2 (geographic distance does not predict biological distinctiveness) cautions against the siting of mine sites on adjacent seamounts.

Because seamounts in close proximity in the central Pacific do not necessarily have similar benthic assemblages (within a depth stratum), mined seamounts should be dispersed as widely as possible throughout the containment area. Result 3 (marked species turnover at distances > approximately 2 km) suggests that mine sites of 20 km^2 (i.e. > 2 km in linear extent) will encompass multiple ecological communities and hence affect a greater range of ecological features than would smaller-sized mine sites. Although we recognize that smaller mine sites are likely to be less economically efficient (and thus unlikely to be adopted), our result suggests that for conservation purposes they are less likely to impact distinct ecological assemblages.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Diagnostics for sampling effort, depth, investigator and submersible type.

Figure S1 Depth variation in temperature, oxygen and salinity.

Table S1 Summary of site and dive information.

BIOSKETCH

This paper is a joint effort by members of the Data Analysis Working Group (DAWG) of the Census of Marine Life on Seamounts (CenSeam). The chief focus of the group is to apply specialized technical and scientific expertise to questions of deep-sea ecology and conservation, both fundamental and applied.

Author contributions: M.C., A.B., A.R., T.A.S., T.O'H., J.K. and J.D. conceived the ideas; C.K. and A.B. collected the data; T.A.S., T.O'H., A.R., M.C., A.B., J.K. and J.D. analysed the data; T.A.S., A.R., M.C., T.O'H., A.B., J.K. and J.D. led the writing.

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